ostrum, with antennal spines and with an arched median, dorsal, spiny crest on the gastric region. There is no trace either of eyes or even of eye-peduncles. First and third pairs of legs of the usual Crangonine form; second pair non-chelate, rather robust, with fringes of long plumose setæ, their dactylopodites minute, setulose; third and fourth pairs rather more robust than, but similar to, the second, with successively more minute and less gressorial dactylopodites, also furnished with long fringes of plumose setæ. Abdomen compressed, smooth, transversely convex, without spines or carinæ. Telson thin and depressed.

34. *Prionocrangon ommatosteres*, sp. n.

The serrated gastric crest is seven-toothed.

The animal measures in length, from tip of rostrum to tip of telson, about 30 millim., of which the carapace from tip of rostrum to middle of hinder margin is about 10 millim.

A single somewhat mutilated specimen from Station 116, 405 fathoms.

[To be continued.]

XLVIII.—*The Biological Import of Amitotic (Direct) Nuclear Division in the Animal Kingdom.* By H. E. Ziegler, Ph.D., Extra-ordinary Professor of Zoology, Freiburg i. B. *

In W. Flemming's most recent paper † we find the following passage:—"As regards the fragmentation of the nuclei of leucocytes—and amitotic nuclear division in general—it appears to me not impossible that the following view could also be held. The leucocytes, like the cells of other tissues, perform their normal physiological reproduction by means of mitosis; those cells only which have come into existence by this process preserve the faculty of continuing to live and of producing similar cells in the same manner. *Fragmentation of the nucleus, with and without subsequent division of the cell, is universally a process in the tissues of Vertebrates, which*

* Translated from the 'Biologisches Centralblatt,' Bd. xi. nos. 12 and 13, pp. 372–389, July 15, 1891.

† W. Flemming, "Ueber Teilung und Kernformen bei Leukocyten und über deren Attraktionssphären," Archiv f. mikr. Anatomie, 37 Bd., 1891.

does not lead to the physiological multiplication and reproduction of cells, but, on the contrary, represents where it occurs a degeneration or aberration, or perhaps in many cases (formation of multinuclear cells by fragmentation) is subservient to the metabolism of the cell by increasing the periphery of the nucleus. According to this theory, therefore, if leucocytes divide with fragmentation of their nuclei, the products of this process would no longer be material possessing reproductive power, but, on the contrary, would be destined to destruction, although they may still be able to continue to live for a long time in the tissues and juices."

Although Flemming writes the foregoing sentences merely as probable hypotheses, and not as proved results, they are nevertheless of great importance, and Flemming's development of his theme will largely contribute towards bringing into general recognition the true interpretation of amitotic nuclear division *. For many years past I have cherished a similar view with regard to the biological import of amitotic nuclear division to that which is expressed in the above-quoted sentences of Flemming, and I have since found it confirmed in all cases of amitotic nuclear division which have come under my notice in literature; I therefore believe that amitotic nuclear division, wherever it appears, is to be interpreted in the sense of the exposition which I have just cited.

The study of the nuclei in the periblast of Teleostei had been my starting-point in such considerations †. "The nuclei in the periblast of Teleostei divide at the time of segmentation by karyokinesis, as a number of authors agree in affirming; subsequently, however, they acquire a peculiar appearance ‡, and exhibit the figures of direct nuclear

* Amitotic nuclear division includes, according to Arnold's terminology, "direct segmentation," "direct fragmentation," and "indirect fragmentation." I disregard Arnold's designations entirely, since, as it appears to me, they are based upon an unnatural classification.

† E. Ziegler, "Die Entstehung des Blutes bei Knochenfischembryonen," Archiv f. mikr. Anatomie, 30 Bd., 1887, p. 160.

‡ The same phenomena are seen not only in the case of the nuclei of the other meroblastic Vertebrates which lie in the yolk, but also in that of the yolk-contained nuclei of the Arthropods. Just as in the development of the meroblastic ova of Vertebrates it is in the highest degree improbable, and at least not yet proved, that the large nuclei lying in the yolk take any morphological share whatever in the building up of the embryo, so the same assertion can be maintained for those nuclei which in the Arthropods still remain in the yolk after the formation of the blastoderm and of the rudiment of the primitive streak. I quote the observations of Graber on this point ("Vergleichende Studien über der Embryologie der Insekten und insbesondere der Musciden," Denkschriften der k. Akademie zu Wien, Math.-naturw. Klasse, 56 Bd., 1889):—

division." In my previous paper I dilated upon the fact that "in cases of a widely different character we find peculiar forms of nuclei, which we may class together with the nuclei of the periblast of Teleosteans, and that these phenomena constitute an important chapter for the natural history of the cell-nucleus in general." "It would seem fitting were we to use the expression fragmentation in the animal kingdom (and, indeed, in the first place only for the Metazoa) for those morphologically and physiologically associated cases which are characterized as follows. The nuclei are considerably larger than the ordinary nuclei in the same animal, and exhibit an abnormal poverty, or an abnormal distribution, of chromatin. The nuclei multiply by direct nuclear division; it often happens that the division is not carried as far as the separation of the segments, so that the nuclei show bud-like processes and irregular prolongations, or appear divided by constrictions. Fragmentation occurs in cells which no longer undergo division, or in masses of protoplasm which have arisen through incomplete cell-division (*i. e.* through nuclear division without concomitant division of the cell). The appearance of fragmentation is connected with the fact that the cell has become specialized, has adapted itself to a definite physiological function, that, for instance, it is harbouring and assimilating food-yolk, is performing some process of secretion or absorption, &c. The nuclei have degenerated, in so far as the cell is no longer capable of division, and consequently can no longer morphologically take part in the further building-up of the embryo or in processes of regeneration; if in this sense we designate the nuclei as degenerate, this does not preclude them from performing their physiological function for a longer or shorter time. There are simpler modes of degeneration which lead to speedy destruction; fragmentation only occurs when the nuclei first undertake a specialized function and then perish."

"Within the blastoderm, scattered about in the yolk, are found, as is well known, in the Muscidæ, as well as in all Insects hitherto investigated, cells, or at least nuclei, which we consequently very frequently term yolk-cells ("Vitellophaga," according to Nussbaum). Now as regards the share which these much-discussed cells take in the building-up of the embryo, at present far the most generally accepted view is that they merely assist in the assimilation of the yolk, and that, although they and the cells of the blastoderm have a common origin, the former elements take no special part in the formation of tissues, and are not to be included in the category of the 'true germinal layers.' The vitellophaga of the Muscidæ are nuclei without a plasma-envelope, and appear "as generally very irregularly defined or amœboid structures of relatively gigantic size."

According to the present stage of our investigations we may assert that *the amitotic division of the nucleus always indicates the end of the series of divisions.* Where this mode of division appears, only a limited number of divisions, or only very few, or none at all take place, while the nuclei which divide by mitosis possess an unlimited capacity for multiplication for the whole duration of the life of the individual. It is even *à priori* hardly probable that nuclei which have arisen by amitotic division will ever divide again by mitosis; for in amitotic nuclear division the distribution of the chromatin takes place in a rough and usually very irregular fashion; in consequence of this, mitosis, which effects a methodical and altogether equable division of the chromatin, would subsequently have no importance at all and no further value, or it would at least remain quite unintelligible.

Flemming shows (*loc. cit.*) that, in the amitotic division of the nuclei of leucocytes, *in connexion with the constriction of the nucleus a division of the attraction-sphere and of its central body does not take place* *. Into connexion with the absence of this division it is perhaps possible to bring the fact that *division of the cell does not usually follow amitotic nuclear division.* As Flemming remarks, further investigations will have to decide whether, in those cases in which amitotic

* This observation gives an important support to the view that the processes of amitotic nuclear division and of branching of the nuclei are connected with and merge into one another; the unusual size also is a feature common both to the nuclei which are branched and to those which divide without mitosis. Korschelt ("Beiträge zur Morphologie und Physiologie des Zellkerns," Zool. Jahrbücher, Abteilung für Anat. und Ontogenie, Bd. iv., 1889) has shown in comprehensive fashion that branched nuclei frequently occur in cells such as those in which an intense secretion takes place. The branching of the nuclei points to the fact that they have adapted themselves to a large extent to the specialized physiological function, and this far-reaching adaptation involves the destruction of the nuclei after a longer or shorter interval. That there is a physiological and morphological connexion between the amitotic division and the branching of the nuclei is also to be deduced from the fact that they frequently occur side by side; for instance, in some preparations of the whole of the alimentary canal of *Porcellioscaber* (which Dr. vom Rath most kindly allowed me to examine) I observed that the nuclei of the epithelium of the posterior half of the mid-gut exhibited manifold ramifications and here and there the figures of direct division. I would remark in passing that forms of nuclei such as we meet with in this instance have been described and figured by van Bambeke ("Des déformations artificielles du Noyau," Archives de Biologie, t. vii., 1887), but that I am unable to discuss his paper further, because I am not perfectly clear as to what van Bambeke wishes to convey by the expression "Déformation artificielle."

It will perhaps be advisable to make a subdivision for those cases of amitotic nuclear division which occur in conjunction with branching of the nuclei.

division is accompanied by a division of the cell, a division of the attraction-sphere takes place.

According to all the investigations which have hitherto been made, it is a matter of certainty that *those nuclei which divide without mitosis are always distinguished by their excessive size**. This peculiarity appears also to occur in the case of the leucocyte-nuclei which divide without mitosis, although it is not so noticeable here as elsewhere. The unusual size is undoubtedly connected with the physiological function, and, in my opinion, it is permissible to advance the hypothesis that in the Metazoa *amitotic nuclear division occurs (chiefly, perhaps exclusively) in such nuclei as minister to a process of unusually active secretion or assimilation.* With regard to this theory, I will now consider a few cases of amitotic division.

The regressive changes which set in in the egg-cells in the vertebrate ovary take place with the help of leucocytes, which creep into their interior, and of cells which penetrate the outer wall of the egg-cell from the epithelium of the follicle, which has become multilamellar; the nuclei of the cells which effect the absorption of the egg-cell degenerate while continuing to increase in size, and exhibit amitotic division. The physiological conditions in this instance are the same as in the nuclei in the yolk of meroblastic Vertebrates, in so far as it is

* In some cases large nuclei of this kind have had the term "*giant*" applied to them. It would be advisable always to employ the same name for all unusually large nuclei occurring in the Metazoa (with the exception of the nuclei of the genital cells). In this sense we could generalize the expression "giant nucleus." The term macronucleus, which is employed in speaking of the ciliated Infusoria and Acinetaria, should not be transferred to the Metazoa, for, indeed, the Protozoa in question occupy a position quite by themselves with reference to nuclear conditions. For the type of unusually large nuclei which is found in the Metazoa I would propose the name "*meganucleus.*" Recent discoveries may then be stated very briefly as follows:—Where meganuclei occur there takes place a process of active secretion or assimilation; meganuclei can divide without mitosis, and amitotic nuclear division among the Metazoa occurs only in meganuclei; meganuclei have only a limited capacity for division, and always perish after a time.—It would be advisable to give the nuclei of the genital cells an exceptional position, and not to include them among the meganuclei. It is true that the nucleus of the ovum, adapting itself to the ovogenetic processes, attains an extraordinary size, but its bulk is capable of diminution; while in the case of a typical meganucleus, so far as we know, mitotic division never again takes place, the nucleus of the ovum undergoes mitotic division in giving rise to the first directive vesicle. In the nuclei of somatic cells the adaptation to a definite physiological function could advance so far as to annihilate the normal faculty for division; in the nuclei of the genital cells this naturally could not take place.

a question of exercising an assimilating influence upon the yolk-material. The changes undergone by the leucocytes and follicle-cells during the absorption of the egg-cell, and especially the enlargement of the nucleus, the manifold forms of the amitotic division, the occurrence of multinuclear cells, and the disintegration of nuclei, have recently been minutely investigated by Ruge* in different Amphibia. Ruge's paper contains so many observations of importance for the question before us that I must refer the reader to it, and cannot here attempt to recapitulate his results in a few words.

A very typical case is that which has been described by Chun †. In the nectocalyces of the Calycophorid Siphonophora we find in the radial canals and in the anastomosing offshoots from them "the large flattened endoderm-cells filled with a brood of nuclei." "The larger ones among them rarely exhibit rounded contours; generally they show a band-like or vermiform elongation, and are beset with lateral papillæ." "Sometimes dumb-bell- or biscuit-shaped nuclei constrict into two equal halves, while at others the division of the nucleus more resembles a budding, in so far as the nucleus which is constricted off is considerably smaller, while the larger nucleus simultaneously exhibits various proliferations, which likewise commence to constrict." "In no case does the direct division of the nucleus in the Siphonophora entail a subsequent division of the cell;" Chun lays special stress upon this fact, "since, moreover, in all cases where direct nuclear division has hitherto been shown to exist we get a formation of multinuclear cells, but no certain evidence of a subsequent division of the cell." It appears to be probable that the nuclei described by Chun possess an energetic physiological activity of the kind mentioned above; for the formation of the plexiform anastomosing offshoots of the radial canals points to the fact that the epithelium of these canals is destined to come into contact with the surrounding tissues to the largest possible extent, and, as Chun asserts, is of great importance for the metabolism of the musculature of the nectocalyces which effects the swimming-motion.

In many insects we find nuclei of quite remarkable size in the nutritive cells, which collect round the egg-cell in the ovary in order to supply it with nutrient material ‡; in

* G. Ruge, "Vorgänge am Eifollikel der Wirbeltiere," Morphologisches Jahrbuch, xv. Bd., 1890.

† C. Chun, "Ueber die Bedeutung der direkten Kernteilung," Schriften der physikal.-ökon. Gesellschaft zu Königsberg i. Pr., 31 Jahrg., 1890.

‡ Compare also the figure of the large nutritive cells of *Musca vomi-*

nutritive cells of this kind in the terminal chamber of the ovaries of different species of bugs Korschelt * has observed the figures of amitotic nuclear division.

In the follicle epithelium which envelopes the ovum of the mole-cricket ("le tapis cellulaire qui recouvre l'œuf de la taupe-grillon arrivé à l'état parfait") Carnoy † saw amitotic nuclear division and multinuclear cells. Since the cells of the epithelium of the follicle play a great part in the nourishment of the growing egg-cell, and since they lose their importance when the egg-cell becomes fully ripe, the biological conditions which we have emphasized above exist in this case also.

In the large nuclei of the external layers of the embryonic envelope of a Brazilian scorpion direct division has been observed by Blochmann ‡. "A division of the cell in connexion with this division of the nucleus probably never occurs in any case." In none of his preparations did Blochmann find an indication of cell-division; "the absence of cell-division is also attested by the large number of binuclear cells which are found in all parts of the embryonic envelope." "The embryonic envelope is a transitory structure, which certainly undergoes disintegration soon after these divisions." Whether this embryonic membrane has an important physiological function, whether it perhaps secretes a serous fluid which surrounds the embryo, cannot at present be determined.

In *Cyclas cornea* (a small freshwater mussel) I have observed a striking enlargement and peculiar fragmentation in the nuclei of the epithelium of the brood-pouches, which arise in the gills and surround the embryos §. A fluid gradually accumulates in the brood-capsules; a secretory function on the part of the cells is therefore rendered probable. Certain of the epithelial cells separate from the wall and are devoured by the embryos, which continue to grow within the brood-capsules until they attain sexual maturity.

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toria in Henking's paper "Die ersten Entwicklungsvorgänge im Fliegenei," Zeitschr. f. wiss. Zoologie, Bd. 46, 1888.

* Korschelt, "Ueber die Entstehung und Bedeutung der verschiedenen Zellenelemente des Insektenovariums," Zeitschr. f. wiss. Zoologie, Bd. 43, 1886.

† J. B. Carnoy, "La Cystodiérèse chez les Arthropodes," La Cellule, t. i., 1884, p. 219.

‡ Blochmann, "Ueber direkte Kernteilung in der Embryonalhülle der Skorpione," Morphol. Jahrbuch, x. Bd., 1885.

§ H. E. Ziegler, "Die Entwicklung von *Cyclas cornea*," Zeitschrift für wiss. Zoologie, 41 Bd., 1885.

The epithelium of the urinary bladder of different mammals, especially the mouse and the dog, has recently received a minute investigation at the hands of A. S. Dogiel, who writes as follows*:—"In one and the same multilamellar epithelium we find amitotic nuclear division in the cells of the upper layers, and mitotic in those of the remaining layers." "In different mammals, but chiefly in the small Rodents, the uppermost epithelial cells of the urinary bladder are of an extraordinary size, and possess a large number of nuclei." "We see that the process of multiplication of the nuclei in the epithelial cells of the uppermost layers is similar to that which is found in the giant cells, leucocytes, epithelium of the mammary glands, &c., namely direct amitotic nuclear division, or even, more properly speaking, bud-formation." The uppermost cells of the epithelium of the urinary bladder have a secretory function and give rise to the layer of mucus, "which protects the mucous membrane of the bladder from the effects of direct contact with the urine." If we further reflect that in multilamellar epithelia the uppermost layer of cells always undergoes a gradual degeneration and is regenerated from the deeper layers, we see that in the case of amitotic nuclear division before us the biological conditions are perfectly typical †.

In cells which are typical gland-cells amitotic division of the nucleus is not rare ‡. *Gland-cells in which an active secretion takes place always have a considerable bulk and usually a large nucleus* §, *which never divides by mitosis*;

* A. S. Dogiel, "Ueber das Epithel der Harnblase," Archiv f. mikrosk. Anatomie, 35 Bd., 1890.

† Amitotic nuclear division in the epithelium of the bladder has been found not only in Mammals, but also in Urodela. Flemming observed it in the Salamander, but is inclined to regard its occurrence not as normal, but rather as pathological (Flemming, "Amitotische Kernteilung im Blasenepithel des Salamanders," Archiv f. mikr. Anat. Bd. 34, 1890).

‡ The secretion of milk is allied to glandular secretion, yet we cannot regard the milk-cells as typical gland-cells, for the body and the nucleus of the cell are not appreciably enlarged. Nissen (Archiv f. mikr. Anat. Bd. 26, 1886) writes as follows on the subject of milk-cells:—"In hundreds of preparations I have not been able to detect mitoses, in spite of the fact that multiplication of the nuclei is an extremely frequent occurrence. Perhaps, therefore, direct nuclear division takes place in this case. However this may be, the nuclei lying at the inner end of the cell separate from the epithelial cells surrounded by a portion of protoplasm."

§ Korschelt ("Ueber die Bedeutung des Kerns für die tierische Zelle," Sitzungsber. der Gesellschaft naturf. Freunde zu Berlin, 1887, p. 127) writes:—"It is highly remarkable that the bulky nuclei . . . occur precisely in cells which have a secretory function. This may point to the

if amitotic division of the nucleus sets in, it is not usually followed by division of the cell.

In *Triton* (according to Klein *) the figures of amitotic nuclear division are met with in the large gland-cells which clothe (or, more correctly speaking, fill) the sac-shaped dermal glands, and multinuclear cells are also found among them.

In *Anilocra* (an Isopod Crustacean) O. vom Rath † found very large nuclei, which divide without mitosis, in large glandular cells, which in all probability are the salivary glands of the animal; several nuclei are often found in one cell.

We now come to the cases of direct nuclear division which are met with in the epithelium of the alimentary canal of Crustacea and Insects ‡, in the hepatic tubules of Crustacea, and in the Malpighian tubes of Insects. For we have here always to deal with cells of a glandular character.

With regard to the Malpighian tubes, amitotic division was found in the larva of *Aprophora spumaria* by Carnoy § and in *Dytiscus marginalis* by Platner ‖. "The cells of the Malpighian vessels of Insects," writes Platner, "are exceeded in size only by the ova. The diameter of the nucleus is often three times larger, and even more, than that of the cells of the Salamander, and at the same time, in spite of the most vigorous multiplication of cells, necessitated by the consumption which takes place when the organs are doing their work, we find no mitosis. We meet with the greatest difference in the size of the cells; the large cells contain one large nucleus,

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fact that the nuclei are of quite extraordinary importance for such cells, that they exercise a certain influence on the activity of the cell. We receive further support for this conjecture in the fact that the nuclei do not at first possess the considerable circumference and unusual form, but only acquire these when the cells enter upon their functions."

* E. Klein, "Observations on the Glandular Epithelium and Division of Nuclei in the Skin of the Newt," Quart. Journ. Micr. Sci. vol. xix. 1879.

† O. vom Rath, "Ueber eine eigenartige polyzentrische Anordnung des Chromatins," Zoologischer Anzeiger, 1890, p. 334.

‡ In Nematodes also amitotic nuclear division occurs in the epithelium of the alimentary canal. Hoyer found the figures of direct nuclear division and multinuclear cells in the alimentary canal of sexually mature individuals of *Rhabdonema nigrovenosum* (Hoyer, "Ueber ein für das Studium der 'direkten' Kernteilung vorzüglich geeignetes Objekt," Anatom. Anzeiger, 5 Jahrg. 1890, p. 26).

§ J. B. Carnoy, "La Cytodiérèse chez les Arthropodes," La Cellule, t. i., 1884, p. 219.

‖ G. Platner, "Beiträge zur Kenntnis der Zelle und ihre Teilungserscheinungen," Archiv f. mikrosk. Anatomie, 33 Bd.

or two smaller ones, or even three, four, or five; the nuclei themselves are found in all stages of direct division.

The conditions presented by the epithelium of the mid-gut of Insects * and Crustacea require special discussion. After a critical examination of the literature we must arrive at the conclusion that in such epithelial cells as are already functioning as gland-cells, or in which the process of secretion is just beginning, direct nuclear division may occur; that these cells and their nuclei are then gradually or periodically cast off, and that the regeneration of the epithelium usually proceeds from isolated groups of young cells, or from regeneration-pits, the cells of which multiply by mitosis. Frenzel's† observations also admit of interpretation in this sense. This author noticed in the intestinal epithelium of *Phronima* a few scattered islands of younger cells, which were not engaged in secretion and multiplied actively by mitosis. In *Astacus*, *Maja*, and *Dromia* he observed typical amitotic nuclear division ‡. As regards Insects, Frenzel writes as follows:—"The cells of the mid-gut have to perform the task of furnishing the digestive secretion, and a portion of them, namely the true epithelial cells, in the caterpillars the columnar as well as the mucous-cells, constantly perish in so doing" §. "The true epithelial cells in the mid-gut of Insects, it matters not whether they belong to the actual intestinal tube or to its evaginations, or whether they are to be ascribed to the type of elongated columnar cells, or to that of rounded mucous cells, propagate by the method of direct amitotic nuclear division." So far Frenzel's statements agree very well with

* Amitotic nuclear division occurs not only in the mid-gut, but also in the hind-gut of Insects. Faussek ("Beiträge zur Histologie des Darmkanals der Insekten," Zeitschr. f. wiss. Zoologie, Bd. 45, 1887) observed it in the hind-gut of a grasshopper (*Eremobia muricata*, Pall.) and in the rectal glands of *Æschna*-larvæ. So far as we know, this division of the nucleus is not followed by a division of the cell.

† J. Frenzel, "Ueber den Darmkanal der Crustaceen nebst Bemerkungen zur Epithelregeneration," Archiv f. mikrosk. Anat. 25 Bd., 1885; "Einiges über den Mitteldarm der Insekten, sowie über Epithelregeneration," Archiv für mikrosk. Anat. 26 Bd., 1886.

‡ I have noticed in sections of *Astacus* that the nuclei of the epithelial cells of the mid-gut, in certain regions lying in the depths of the folds, have the appearance of young nuclei, which probably divide by mitosis.

§ The way in which the secretion collects in the cells of the mid-gut of Insects, and how such cells, with their nuclei, are cast off into the lumen of the intestine when the secretion is poured forth, has been minutely described by A. van Gehuchten ("Recherches histologiques sur l'appareil digestif de la larve de *Ptychoptera contaminata*," La Cellule, t. vi. 1890). Mingazzini, too, alludes to the casting off of the epithelial cells ("Ricerche sul canale digerente dei Lamellicorni fitofagi," Mitt. a. d. zool. Station zu Neapel, ix. Bd., 1889, pp. 55 and 279).

the theoretical views which may be brought to bear on the point. But Frenzel continues :—" while the specific gland-cells of the pits multiply by the method of indirect (mitotic) nuclear division." Frenzel considers, therefore, that the epithelial cells multiply by amitotic division, the gland-cells by mitosis, and this view stands in abrupt contradiction to the statements above. The state of the case is very easily explained when we consider that the cells of the pits, which divide by mitosis, furnish not the slightest grounds for being regarded as gland-cells; the body of the cell is small and contains no drops of secretion. Much more light is consequently thrown upon the matter by regarding the pits not as glandular, but as regenerative, and assuming that the " true epithelial cells" are regenerated and thrust forward therefrom. In *Periplaneta orientalis*, L., I have by the study of sections convinced myself of the justice of this view.

We should therefore have no grounds whatever for the assumption, were we to conclude that in the intestinal canal of Crustacea or Insects the multiplication of cells is based upon amitotic nuclear division, and it appears, on the contrary, that amitotic nuclear division only occurs in such cells as are in the act of functioning as gland-cells and which sooner or later will perish in so doing. It may here be also mentioned that in many Arthropods there takes place at a certain time a shedding of the whole glandular epithelium of the mid-gut. According to Bizozzero (Atti della R. Accad. d. Sc. di Torino, vol. xxiv. 1888–89, p. 702) in *Hydrophilus piceus* the whole epithelium of the mid-gut is shed every two to five days, and the new epithelium is formed from the " intestinal glands " (regeneration pits) by protrusion and metamorphosis of the cells. In Polydesmids it was observed by O. vom Rath * that during ecdysis the epithelium of the mid-gut is shed and regenerated. In Hymenoptera the epithelium of the mid-gut is renewed during the pupa state (*vide* Frenzel, *loc. cit.* p. 257). The dissolution of the existing mid-gut epithelium in the pupa stage of the Muscidæ has long been known owing to the fundamental investigation of Weismann †, and the development of the new epithelium has recently been described by Kowalevsky ‡ and van Rees §. The latter writes as

* O. vom Rath, "Ueber die Fortpflanzung der Diplopoden (Chilognathen)," Berichte der naturf. Gesellschaft zu Freiburg i. B., Bd. v., 1890, p. 13.

† A. Weismann, " Die nachembryonale Entwicklung der Musciden," Zeitschrift f. wiss. Zoologie, 14 Bd., 1864.

‡ A. Kowalevsky, " Beiträge zur Kenntnis der nachembryonale Entwicklung der Musciden," Zeitschr. f. wiss. Zoologie, 45 Bd., 1887.

§ J. van Rees, " Beiträge zur Kenntnis der innern Metamorphose von

follows:—"The whole internal epithelial tube, as well as a number of smaller cells which I am inclined to regard as connective tissue, is cast off into the lumen. Only a number of epithelial islets remain behind, nestling closely against the at present undissolved larval muscular layer."

According to Carnoy (*loc. cit.*) amitotic nuclear division in the Arthropods is also met with in the nuclei of the muscle-fibres and in the nuclei of the testicular tubes. Carnoy maintains that in fully-developed muscle-fibres of all Arthropods he invariably observed direct nuclear division only*; from this we can raise no objection against the views represented above, since it is easily conceivable that the nuclei of mature muscle-fibres adapt themselves to their special physiological functions. As regards the nuclei of the testicular tubes, we must naturally strictly distinguish whether the amitotic division occurs in the nuclei of spermatogonia or in those of the supporting- (companion- or fluid-furnishing [Begleit- oder Saft-]) cells which have a secretory function. In the latter amitotic division may be expected; but certain statements exist, according to which it occurs in spermatogonia; these cases must be submitted to fresh investigation. As Dr. vom Rath is at present working at this question in the Zoological Institute here, I will not further discuss it †.

We shall not be surprised to find that amitotic nuclear division occurs in the cells of the fat-body of Arthropods; for these cells, in their physiological function, are adapted to the storing-up of nutritive material, and disintegrate if the nutritive material is used to build up other tissues. Carnoy (*loc. cit.*) describes the amitotic division of the nuclei of cells of the fat-body, and mentions that, in consequence of the absence of cell-division, cells with several nuclei (from two to

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Musca vomitoria," Zool. Jahrbücher, Abt. für Anat. u. Ontog., iii. Bd., 1889.

* With reference to the direct nuclear division observed in the muscle-cells of Vertebrates, Flemming declares (*loc. cit.* p. 290) that it plays no part in the physiological growth of the muscles, and that the amitotic multiplication of nuclei occurring in the pathological regeneration of muscle-fibres has the value of a phenomenon of degeneration. As supplementing this I may further refer to Robert's paper, "Versuche über die Wiederbildung quergestreifter Muskelfasern" (Ziegler's Beiträge zur pathol. Anatomie und allgem. Pathologie, x. Bd., 1891, p. 169), according to which, in the multiplication of cells which give rise to the young muscle-fibres, mitotic division exclusively occurs.

† I refer the reader to the communication from O. vom Rath, which is about to appear in the 'Zool. Anzeiger,' on "The Import of Amitotic Nuclear Division in the Testis" ("Die Bedeutung der amitotischen Kerneteilung im Hoden").

ten) are frequently met with *. The consumption of the cells of the fat-body has been minutely observed by van Rees (*loc. cit.* pp. 76–83) in the pupa of *Musca vomitoria*. "It is not only the muscles of the larva," he writes, "which are utilized as food by the leucocytes of the pupa. I have found that the fat-cells also are attacked by them, serve them as food, and are at any rate partially destroyed by them. On the third day I was able, by examining sections, to recognize with certainty the presence of a small number of blood-corpuscles in the interior of these fat-cells. Most of them lay in the immediate neighbourhood of the nucleus, some few in the protoplasmic net of the fat-cell between the small fat-granules. In some blood-corpuscles I found from two to three nuclei, or even six or a still larger number. On the sixth day more than a hundred leucocytes were collected round the nucleus of the fat-cell; the nucleus steadily loses stainable matter, so that the idea naturally arises that the latter is dissolving and is being conveyed to the blood-corpuscles by osmosis. It is not until several days have elapsed that a portion of the fat-cells disappears, and another portion later still. The leucocytes now disperse through the fluid of the body, and we are then able to distinguish, besides leucocytes with only a single nucleus, others which possess several nuclei, even as many as twelve."

Among the Worms, we find in the *Echinorhynchi* a typical example of amitotic nuclear division. According to Hamann's † careful description the nuclei of the dermal layer and those of the lemnisci grow to an enormous size and frequently exhibit branched and lobate forms. Constriction into two equal or unequal parts or resolution into several fragments frequently occur. Since the limits of the cell have disappeared there can be no question of a division of the cell following on division of the nucleus. The function of the nuclei is manifestly that of assimilation; for, as is well known, the *Echinorhynchi* possess no alimentary canal, and are nourished by osmosis through the skin; vacuoles are formed in the dermal layer which coalesce into a lacunar system; the lemnisci, which have arisen as local thickenings of the dermal layer, are traversed by large cavities, which are

* In Vertebrates, too, we find several nuclei in the fat-cells in many kinds of absorption of fat (Flemming, Archiv für mikrosk. Anatomie, Bd. 7, 1871, pp. 71, 330, 357, note; and Virchow's Archiv, 1872). Since the observations in question date from an earlier period, in which no attention was as yet paid to the difference between mitotic and amitotic division, the case in this respect is not yet clear.

† O. Hamann, "Monographie der Acanthocephalen (Echinorhynchen)," Jenaische Zeitschrift, 25 Bd., 1890, pp. 140 and 215.

connected with the lacunæ of the dermal layer of the neck and proboscis. Since the proboscis and the neck are buried in the intestinal wall of the host, and the rest of the body in the lumen of the intestine is surrounded by the contents of the latter, nutrition can be carried on by means of the lacunar system of the proboscis, the neck, and the lemnisci, as well as that of the remainder of the dermal layer. The lacunar system of the lemnisci has, moreover, a hydrodynamic importance for the extension and retraction of the proboscis.

According to Kückenthal* direct nuclear division occurs in the Annelids, in the "lymphoid cells," which float in the body-cavity; many of these cells contain two or four nuclei. Kückenthal considers that the direct division of the nucleus is followed by division of the cell, and he believes that the quadrinuclear cells divide into four uninuclear ones. According to his view the cells which have arisen in this way apply themselves to the dorsal vessel and to the intestine, and change into chloragogen-cells †, which then finally perish by being set free and degenerating. It appears to me that the question of the regeneration of the lymphoid and chloragogen-cells is not yet completely explained by these observations.

In the uterus of Mammals, in the processes which follow the setting-in of pregnancy, especially in the formation of the placenta, amitotic nuclear division occurs in various tissues. We learn from the papers of Masius ‡ and Minot § that in the rabbit fragmentation of the nuclei and multinuclear cells occur in the degenerating uterine epithelium, and that in the endothelium cells of degenerating walls of vessels large fragmented nuclei and peculiar groups of nuclei, pointing to direct nuclear division, are met with. I discuss these phenomena no further, since it would be too difficult and would lead us too far astray to investigate to what extent processes of absorption and secretion are operating in these cases.

The cases of amitotic nuclear division which belong to the domain of the pathologists, especially the nuclear division in

* W. Kückenthal, "Ueber die lymphoiden Zellen der Anneliden," Jen. Zeitschrift f. Naturw. 18 Bd., 1885.

† This statement of Kückenthal's contradicts Vejdovsky's observation ('System und Morphologie der Oligochäten,' Prag, 1884, p. 112), according to which the regeneration of the degenerating chloragogen-cells proceeds from small young cells which lie deep down between the large cells.

‡ J. Masius, "De la Genèse du Placenta chez le lapin," Archives de Biologie, t. ix., 1889.

§ Ch. Sedgwick Minot, "Uterus and Embryo.—I. Rabbit: II. Man," Journal of Morphology, vol. ii., 1889, Boston, Mass.

the giant cells *, which are met with in the spleen, in the marrow of the bones †, and in tumours, I leave entirely on one side.

From all the statements which have been brought forward the reader will have perceived that in the Metazoa amitotic nuclear division only occurs in those cases in which the nuclei have adapted themselves to a special function; it always points to the approaching dissolution of the nuclei. Waldeyer ‡ is of the opinion that the amitotic method of division is the primary one, as being the simpler. The cases which occur in the Metazoa are totally unfitted to support this view; *amitotic nuclear division in the Metazoa always appears as secondarily acquired.* We have yet to discuss the occurrence of amitotic nuclear division among the Protozoa.

Since karyokinesis occurs with such striking agreement in the whole of the animal and the whole of the vegetable kingdom, we may accordingly conclude that this process is phylogenetically a very old one, and was already generally distributed in the common ancestors of animals and plants. In agreement with this is the fact that mitotic division is observed in almost all classes of the Protozoa. Among the Rhizopods it has been clearly established for *Euglypha* §, and among the Heliozoa for *Actinosphærium* ‖; among the Radiolaria, too, it appears not to be absent, for Brandt ¶ has observed in the case of the small nuclei of the Sphærozoids a spindle-shaped transformation during division. Among the Flagellata Bütschli has seen in *Euglena* during the division

* I cannot venture to enter into the discussion of the obscure physiological import of the giant cells; I refer the reader to Flemming's statements (Archiv f. mikr. Anatomie, Bd. 37, p. 292). The occurrence of direct nuclear division and of the formation of giant cells in the marrow of the bones and in tumours has recently been treated of in Strübe's paper, "Ueber Kernteilung und Riesenzellenbildung in Geschwülsten und im Knochenmark," Diss. vorg. d. med. Fakultät zu Freiburg i. B., 1890.

† In many animals (*e. g.* the mouse) the occurrence of giant cells in the spleen and in the marrow of the bones is so regular as to lead us to regard it as the result of a normal rather than of a pathological process.

‡ Waldeyer, "Ueber Karyokinese und ihre Beziehungen zu den Befruchtungsvorgängen," Archiv f. mikrosk. Anatomie, 32 Bd., 1888, p. 44.

§ Schewiakoff, "Ueber die karyokinetische Kernteilung von *Euglypha alveolata*," Morphol. Jahrbuch, 13 Bd., 1887.

‖ A. Gruber, "Ueber Kernteilungsvorgänge bei einigen Protozoen," Zeitschrift f. wiss. Zoologie, Bd. 38, 1883. – R. Hertwig, "Ueber die Kernteilung bei *Actinosphærium Eichhorni*," Jenaische Zeitschrift, Bd. 17, 1841

¶ K. Brandt, "Die koloniebildenden Radiolarien (Sphærozoen)," Fauna und Flora des Golfes von Neapel, xiii. Monographie, Berlin, 1885.

of the nucleus "a distinct spindle, with delicate nuclear plate," and he is of the opinion that nuclear division in the Flagellata "in general approaches the so-called indirect nuclear division" *. Among the Ciliate Infusoria the micronuclei always divide with mitosis †.

If we now wish to consider amitotic division in the Protozoa we must first make a strict distinction between those Protozoa which at the same time contain both a macro- and a micronucleus and those in which only a single kind of nucleus is present. In the former the amitotic division of the macronucleus is an established fact, among the latter I know of no case in which amitotic division was incontestably and indubitably proved. As it is only since the commencement of the eighties that Protozoa have been treated by such methods of conservation and staining, that the disposition of the chromatin in the division of the nucleus can be made out ‡, no weight can be attached to any statement of earlier date. I am also unable to attach any great weight to the more recent observation of Brandt (*loc. cit.*), that direct nuclear division occurs in the formation of swarm-spores of Sphærozoids, having regard to the fact that in such small nuclei the chromatin elements and the outline of the spindle are difficult to see, and that in consequence of the smallest imperfections in preparation the former may become clotted together.

If we now turn to the Ciliate Infusoria and the Acinctaria, in which a micronucleus (small or secondary nucleus ["Kleinkern, Nebenkern"]) and a macronucleus (large or primary nucleus ["Grosskern, Hauptkern"]) exist, and consider the morphological properties and the function of the macronucleus, we shall find that between the macronucleus of the Protozoa and the meganucleus of the Metazoa (*cf.* p. 366, note) manifold analogies § exist. The macronucleus

* Bronn's 'Klassen und Ordnungen.—I. Bütschli, Protozoa; II. Abt. Mastigophora,' p. 742.

† In *Opalina ranarum*, in which, so far as we at present know, only a single form of nuclei, and not both kinds, occurs, mitotic division has been distinctly described by Pfitzner ("Zur Kernteilung bei den Protozoen," Morphol. Jahrbuch, Bd. xi.).

As the contour of the nucleus in this instance is always distinct during the mitosis, and consequently by the application of a faulty method of staining the division would appear to be direct, we have the greater right to submit the statements as to direct nuclear division in Protozoa to a severe criticism.

‡ The development of the methods of preserving Protozoa and staining their nuclei is marked by the publications of A. Certes (Compt. Rend. Acad. Sc. Paris, t. lxxxviii., 1879), E. Korschelt (Zool. Anzeiger, no. 109, 1882), Landsberg (Zool. Anzeiger, no. 114, 1882), and A. Gruber (Zeitschr. f. wiss. Zoologie, Bd. 38, 1882).

§ The macro- and meganucleus have arisen in two independent ways.

of the Protozoa is of the greatest importance for nourishment and growth *. It is distinguished by its remarkable size †, and in large Protozoa assumes a branched shape or that of a ribbon or wreath of roses. With regard to the distribution of chromatin it exhibits a certain similarity to the meganuclei of the Metazoa. The process of division may be simply described as direct, or, with reference to the longitudinal streaking and finely fibrillar structure which appears in the dividing nucleus, as an intermediate stage between mitotic and amitotic division. It is very probable that the number of possible divisions is not unlimited, and that, as stated by Bütschli and Maupas (*loc. cit.* p. 400), on the basis of breeding-experiments, conjugation must set in from time to time, when the existing macronucleus undergoes dissolution ‡ and is replaced by one newly formed. As in the Metazoa, so therefore in the Protozoa also, amitotic division appears only in the case of those nuclei which perish after a certain time; it is true that a large number, even several hundreds, of divisions may ensue before regeneration becomes necessary, while among the Metazoa amitotic division indicates the near

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We may not speak of an homology, because the Ciliate Infusoria and the Acinetaria must be regarded as terminal branches of the Protozoon stem, which grow no higher: the root of the Metazoa does not proceed from these branches of the Protozoa, and to bring the meganuclei of the Metazoa and the macronuclei of the Protozoa into direct phylogenetic relationship with one another is entirely inadmissible.

* Latterly, following the example of Bütschli, the micronucleus has frequently been distinguished as the sexual nucleus, and the macronucleus as the metabolism-nucleus (*vide* Bütschli, 'Protozoa, III. Abt. Infusoria,' p. 1643). Compare also the statements of R. Hertwig, "Ueber die Konjugation der Infusorien," Abhandl. d. k. Akademie, München, II. Kl. 17 Bd., 1889, p. 216 *et seqq.*

† Maupas ("Le rajeunissement caryogamique chez les ciliés," Archives de Zoologie, exp. et gén. 2 sér. t. vii., 1889, x. p. 444) writes:—"An extremely important consequence results from the growth of the new macronuclei. These nuclei in point of fact lose the faculty of dividing by karyomitosis, and henceforward only multiply by simple constriction. At the same time their function, having become purely vegetative, will be confined to the control of nutrition, growth, and agamic multiplication. They have entirely lost the faculty of rejuvenating caryogamy."

‡ Maupas (*loc. cit.* p. 446), writes:—"The mode of eliminating the old nucleus differs slightly according to the species. In *Colpidium* . . . . the whole becomes disorganized at once, and gradually dissolves by a slow absorption, resembling actual digestion. In the Oxytrichidæ, Loxophylidæ, Euplotidæ, and Vorticellidæ this absorption is preceded by a fragmentation; lastly, in the two large *Paramecia* preparation is made for the fragmentation itself by a preliminary unrolling of the nuclear mass, which becomes drawn out into long ribbons." A detailed description of the dissolution of the macronucleus will be found in Bütschli, *loc. cit.* p. 1613.

approach of the end of the divisions; nevertheless it must at the same time be remarked that the amitotic division of the macronucleus runs a more regular course and stands much nearer to mitotic division than the typical cases of amitotic division which occur in the Metazoa.

It would not be quite correct simply to assert that in the Protozoa direct nuclear division is followed by division of the cell, because before a ciliated Infusorian or an Acinetarian divides a double nuclear division takes place—the direct division of the macronucleus and the indirect of the micronucleus *.

It follows from what has been stated that also in Protozoa amitotic division, in so far as we know it at present, is seen not as the primeval method, but as that which is of secondary origin. We have therefore now no empirical ground for the view that indirect nuclear division has originated phylogenetically from direct. The question as to the earliest origin of mitosis leads to that of the earliest origin of the nucleus, and is equally obscure.

Freiburg i. B., Zoological Institute of the University,
April 1891.

Postscript.

A short time before I received the proof-sheets of this paper there appeared M. Loewit's treatise on "Regeneration and Constitution of the White Blood-corpuscles" ("Neubildung und Beschaffenheit der weissen Blutkörperchen," Ziegler's Beiträge zur pathol. Anatomie und allg. Pathologie, 10 Bd., 1891, p. 213), in which it is stated that the cells which float in the blood of the crayfish always exhibit amitotic nuclear division; this nuclear division is frequently followed by division of the cell, but multinuclear cells also occur. It appears to me that no objection can be derived from these observations against the statements which I have made above: for, in the first place, Loewit himself gives a detailed description of the secretory nature of the cells of the crayfish's blood; he mentions that "in the cell-body of numerous cells of the crayfish's blood in the fresh state glistening drop-like structures of varying form and size, and resembling fat, are

* Since in many Acinetaria, and especially in the swarm-spores of *Podophrya*, micronuclei have been shown to exist (*vide* Bütschli, *loc. cit.* p. 1873; Maupas, *loc. cit.* p. 385), the well-known constricting-off of the nucleus in the formation of the swarm-spores of *Podophrya* simply represents the division of the macronucleus.

contained;" he terms the blood-corpuscles simply "unicellular movable glands," and, with reference to the chemical nature of the secretion, "globulin-containing albumen-glands." In the second place, so far as can be judged from his publication, Loewit only examined the blood which flowed from a wound on the body or which was drawn up from between the organs by a pipette; it is consequently a permissible hypothesis that centres for the regeneration of blood-corpuscles exist in the crayfish as in the Insects (see p. 213 of this volume of the 'Biologisches Centralblatt'), which, from a physiological standpoint, would be comparable to the lymphatic glands of Vertebrates, and in which the division of the cells may take place by mitosis. If this is the case it does not appear remarkable that amitotic nuclear division occurs in the blood-corpuscles circulating in the body, which, indeed, have an assimilating and a secretory function. A short time ago Cuénot (Archives de Zoologie, exp. et gén. 2e série, t. ix., 1891, pp. 78 and 83) observed in the crayfish in the gills and in the neighbourhood of the heart "glandes lymphatiques," which he regards as the centres for the regeneration of the blood-corpuscles. I believe therefore that it has not been conclusively proved by Loewit's investigations that a "regenerative" amitotic nuclear division exists. I may incidentally remark that Dr. vom Rath has shown me a series of sections of a young fish-louse (*Cymothoa*, sp., from Naples, 5 millim. long), in which mitotic division of blood-corpuscles was abundantly visible.

XLIX.—*On new Species of* Histeridæ. By George Lewis.

This paper is the seventh of a series published in this Magazine on the Histeridæ, and in the fifth memoir, that of June 1885, the estimate of known species was given as 1485, which included those given in the Munich Catalogue and in Schmidt's List of 1884. Since this assessment was made nearly 450 species have been noticed by various authors; but these figures include those of this paper and 16 of a paper in the press recording new species from Burmah, and do not note any reduction in the general number which may have arisen through the adjustment of the synonymy. Taking the total, then, as it stands now at 1850 species, it cannot be said, as regards their present numbers, that the Histeridæ are a very important family in the Coleoptera; but there are several